Nesom, G.L. 2014. Commentary: Speciation on a local geographic scale in *Mimulus*. Phytoneuron 2014-72: 1–4. Published 14 July 2014. ISSN 2153 733X

# COMMENTARY: SPECIATION ON A LOCAL GEOGRAPHIC SCALE IN *MIMULUS*

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*Erythranthe* (Mimulus) *filicifolia* was recently recognized and formally described as a new species of sect. *Simiola* from Butte and Plumas counties in north-central California (Sexton et al. 2013; transferred to *Erythranthe* by Nesom 2013b). Sexton et al. compared the new species to *E. laciniata*, as both species have a Sierra Nevadan geographic range, generally similar habitats, and dissected leaves. A closely following companion study (Ferris et al. 2014) sought the evolutionary derivation of *E. filicifolia* among *E. laciniata* and two other species of sect. *Simiola*: *E. guttata* (in the broadest sense) and *E. nasuta*. Sequence data for 47 of the total 52 "M. guttatus" populations analyzed by Ferris et al. are from two previously published studies: Sweigart and Willis (2003) and Modliszewski and Willis (2012). The M&W study dealt primarily with annuals, but some perennials were represented (Jen Modliszewski, pers. comm.) — which durations might be included in the Ferris et al. analysis is not explicit and apparently impossible for a reader to determine. Only perennials were represented in the CYCA locus study by Ferris et al. (Jen Modliszewski, pers. comm.) — four of these samples (DUN, LMC, PTR, SIM, as inferred from the S&W data) represent the perennial species *E. grandis*; the rest presumably are *E. guttata* in the strict sense (i.e., rhizomatous, perennial).

To investigate degrees of genetic similarity among the four species, Ferris et al. used clustering via PCA for sequence data and maximum likelihood gene trees for each of seven nuclear loci. On the gene trees, *Erythranthe filicifolia* is positioned completely outside of the other three species as a group; on each of the PCA plots, *E. filicifolia* also is isolated. They concluded (p. 10) that *E. filicifolia* is not closely related to *E. laciniata*, thus it most likely "arose as a completely independent lobed-leaved rock outcrop specialist from some other species like the wide-ranging *M. guttatus*." Because they "were able to only include four species in this analysis, it is not possible to determine its closest relative from our current data." What prevented them from broadening the study's scope is not specified, but a reasonable speculation is that time was allowed only for the original design, which was based on the over-simple assumption that the closest relative of *E. filicifolia* would be among the three species chosen for analysis. It is suggested here that inclusion of only one other species (*E. nudata*), represented by previously published sequence data (e.g., Sweigart & Willis 2003), could easily have been accomodated and would have provided a basis for a more pertinent report.

In the description of *Erythranthe percaulis* (Nesom 2013a) and in making the nomenclatural transfer of *Mimulus filicifolia* to *Erythranthe* (Nesom 2013b, prior to publication of Ferris et al. 2014 and without knowledge of their results), I hypothesized that *E. filicifolia* was probably most closely related to *E. nudata* and *E. percaulis*, both of which also are narrow endemics in the same region as *E. filicifolia*. All three species are annual in duration, completely glabrous to glabrate, and have slightly succulent leaves with prominently reduced surface area. Corollas of *E. nudata* are chasmogamous and allogamous; those of *E. percaulis* and *E. filicifolia* are chasmogamous but very small and probably primarily autogamous (confirmed for *E. filicifolia* by Ferris et al.). *Erythranthe nudata* and *E. percaulis* are restricted to serpentine, while *E. filicifolia* grows mostly on granite outcrops. Of this trio, *E. nudata* and *E. percaulis* are more similar between themselves in overall morphology and habitat and are likely to have a sister relationship. *Erythranthe filicifolia*, in the hypothesis here, is sister to *E. nudata*/*E. percaulis*; an immediate ancestor to this clade may no longer be extant.

With no clear idea of what species *Erythranthe filicifolia* is closely related to and, thus, with no notion of how it might have arisen, one might expect that any related discussion of 'speciation' and 'evolution' would hardly be justified, yet such is the central focus of how the Ferris et al. paper is

advertised (i.e., its title, introduction, a significant part of the discussion, and its conclusion). The rationale that *E. filicifolia* evolved through "local speciation" comes down to simply this (p. 10): "The narrow geographic range of [*E. filicifolia*] compared with other members of the *M. guttatus* species complex from which it might be derived is consistent with it being a product of local speciation." Presumably the phrase "members of the *M. guttatus* species complex from which it might be derived" refers neither to *E. guttata* nor *E. nasuta* (nor *E. grandis*).

Ferris et al. note that "it is not known whether *Mimulus filicifolius* is genetically distinct and/or reproductively isolated from *M. laciniatus*, or whether it is simply a morphologically divergent variety" (p. 2). [Had they found lack of genetic distinction or reproductive isolation, would they then have disavowed recognition of *M. filicifolius* at species rank? Does geographical disjunction provide reproductive isolation? Does distinct morphology imply genetic distinction? Presumably these questions were at least intuitively considered in the initial assessment of Sexton et al.] In seeking a more complete knowledge, the "three main questions" of the Ferris et al. study are stated as these: "(i) Does the recently described *M. filicifolius* differ from *M. laciniatus* in ecology, mating system or genome size as well as in morphology? (ii) Is *M. filicifolius* genetically distinct from *M. laciniatus*? (iii) Is *M. filicifolius* reproductively isolated from *M. laciniatus* or other members of the M. guttatus species complex?" These questions, however [which are answered (i) yes, (ii) yes, and (iii) yes], are related to the strength of definition of *M. filicifolius* as a species — the answers contribute little to an understanding of the process of speciation in the particular case of *M. filicifolius*.

In sum, the main points of Ferris et al. (2014) are essentially (1) that in agreement with Sexton et al. (2013), and adding further details of evidence, they conclude that *Erythranthe filicifolia* is a distinct species but that they do not know where its phylogenetic relationships lie, and (2) that because it has a narrow geographic range relative to some other species (*E. guttata*, *E. microphylla*, and *E. grandis* are not pertinent), it is consistent with "speciation on a local geographic scale."

**Local speciation**

The introduction of Ferris et al. begins with a contrast between vicariant speciation, where an barrier divides a widespread population system and the correspondingly isolated systems diverge evolutionarily, and local speciation, where small populations split off from a large-ranged progenitor species. They note that the highly restricted geographical range of *Erythranthe filicifolia* makes it "an excellent candidate for local speciation." Absence of evidence in support of this model for *E. filicifolia*, however, reduces their analysis to a tautology: If a species has a relatively local geographic range, then it arose through "local speciation." At face value, using the same logic, the corollary of this seems to be that widely distributed species arose through vicariant speciation.

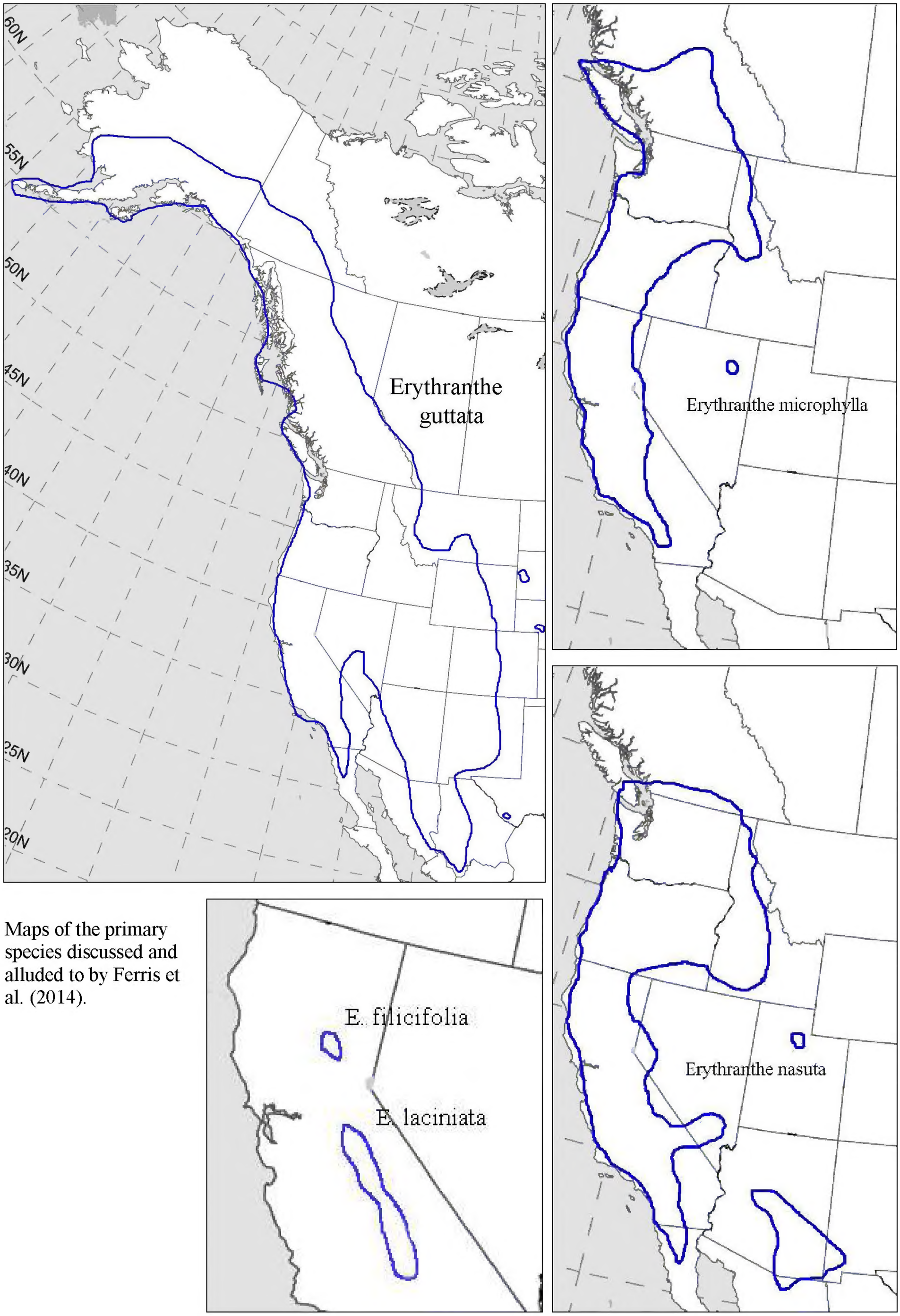
It is entirely possible, without logical or biological constraint, that a species of restricted geography may undergo a vicariant-like event that divides the original population system into two. One of the resultant species might or might not retain the original morphology and biology. Such is what is postulated here for the putative sisters *Erythranthe nudata* and *E. percaulis*.

In anticipation of further discussions of speciation modes that might be similar to that of Ferris et al., here is a geographical accounting of the North American species of *Erythranthe* sect. *Simiola*. The division into three size classes is arbitrary but nonetheless generally indicative of the range of variation. Maps in Nesom & Fraga (2014) provide the bases for these size class assessments.

Narrowly distributed species (1–6 counties or municipios)
arenicola, brachystylis, charlestonensis, chinatiensis, filicifolia, glaucescens, lagunensis, marmorata, michiganensis, nudata, pardalis, percaulis, regni, scouleri, thermalis, visibilis

Moderately distributed species (7–20 counties or municipios)
brevinasuta, caespitosa, corallina, hallii, inamoena, laciniata, minor, parvula, pennellii

Widely distributed species (21 to 100's of counties or municipios)
arvensis, calciphila, cordata, decora, dentiloba, geyeri, glabrata, grandis, guttata, madrensis, microphylla, nasuta, pallens, tilingii, unimaculata, utahensis




Maps of the primary species discussed and alluded to by Ferris et al. (2014).

***Erythranthe guttata* as an ancestral species**

"Because of its wide geographical range and high levels of intraspecific genetic diversity it is likely that *Mimulus guttatus* is the progenitor of the other self-fertilizing species with restricted ranges. This makes the *M. guttatus* species complex excellent for the study of the genetics of recent and local geographical speciation" (Ferris et al., p. 9). Response: an assumption that *E. guttata* is the progenitor of "the other self-fertilizing species [of sect. *Simiola*] with restricted ranges" is ad hoc, with zero underlying evidence. Equally plausible is this statement: *Erythranthe guttata* has spread into a wide geographical range as a result of high levels of intraspecific genetic diversity acquired, via hybridization, from genomic elements of other species. And this: *Erythranthe guttata* and *E. microphylla* are closely related species (but not sister or progenitor-derivative) with considerable gene flow between them, resulting in high levels of intraspecific genetic diversity — *E. guttata* has spread into a relatively wider geographical range because of its ability to reproduce asexually. Etc. Of course, the Ferris et al. assumption may prove to be correct when a species-level phylogeny is objectively documented, but I am aware of many widespread and variable species, over many different genera and families, that are unlikely to be ancestral within their group of close relatives.

As noted above, "*Mimulus guttatus*" in the Ferris et al. study refers to plants that are annual in duration (i.e., *Erythranthe microphylla*) as well as perennial (mostly *E. guttata* but also *E. grandis*). In contrast, the crude map in Figure 1 of Ferris et al. (which gives no indication of how those distributions were determined) apparently is intended to depict the range of the rhizomatous form, i.e., *E. guttata* in the strict sense, or at least to include it (the map also can be construed to include *E. grandis* within the range of *Mimulus guttatus*). Maps 1–4 above are derived directly from county-level distributions developed from revisionary studies of sect. *Simiola* (Nesom 2012, and follow-up studies). The range of *E. guttata* encompasses all of the others (it covers about 3 times the area of that of *E. microphylla*); from mid British Columbia northward, diploids and tetraploids occur in sympatry. The ranges of *E. microphylla* and *E. nasuta* are similar but *E. nasuta* has a greater areal extent and ranges more widely in the southwestern USA, while *E. microphylla* extends further north into British Columbia; *E. filicifolia* is a narrow endemic; *E. laciniata* has a moderate distribution (in the sense above).

## ACKNOWLEDGEMENTS

Many thanks to the late Dr. Tommy Flanagan for help in approaches toward integrating complexity and resolving discordance.

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